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COMPARATIVE MORPHOLOGY OF THE EAR.

THIRD ARTICLE.

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We have next to pass in review several series of organs, which are by no means homologous with one another, although the common function of audition has been assigned to them all. We shall speak, *first*, of the paired otocysts of worms, which are to be regarded as homologous with those of molluscs; *second*, of the unpaired otocyst of the *Turbellaria* and *Tunicata; third*, of the auditory hairs of crustacea; *fourth*, of the tympanal organs of the Orthoptera.[1] This will end what we shall have to say of the invertebrates.

What relation, if any, the unpaired otocysts may have to the paired it is impossible to decide at present. The former may be the product of the fusion of the latter, or they may have arisen independently. Nor is there any reason for associating the otocyst of Turbellaria with that of Tunicata, except that both are single, and placed in the median line so as to connect directly with the brain.

5. Paired Otocysts of Worms.

The earliest discovery of paired auditory vesicles in worms, with which I am acquainted, is due to Stannius (IX., 379), who described in *Arenicola piscatorum* two *Knöpfen* containing crystals, and placed at

[1] This is necessarily deferred until the next article.

the sides of the œsophageal ring. Shortly after Stannius' publication Siebold (VIII.) pointed out the analogy of these "Knöpfen" with the otocysts of molluscs. Similar observations were afterwards made on other *Annellida* by Quatrefages,[1] who also added to his observations in 1850 (VII.), and again in 1870 (VI.). Besides these we have to mention the incidental references by Claparède (I.) and Leydig's brief notices (III. et al.).[2]

Among Nemertines they were discovered by Gräffe, and subse-

[1] Quatrefages: Compt. Rendus Acad. Paris., XIX. (1844), p. 195. See also Ann. Sci. Nat., II. (1844), p. 94.

[2] The following are the principal articles to be consulted: —

I. Claparède, Edouard: Glanures zootomiques parmi les Annélides de Port-vendres (Pyrénées orientales) (Otocystes, pp. 495 and 500).
Mém. Soc. Phys. Genève, XVII. (1864), 463–600. 8 Pls.

II. Keferstein, Wilhelm: Untersuchungen ueber niedere See-thiere (Nemertinen, p. 51, — Otolithenblasen derselben, p. 85).
Zeit. wiss. Zool., XII. (1862), pp. 1–48. Taf. I.–XI.

III. Leydig, Franz: Anatomische Bemerkungen ueber Carinaria, Firola und Amphicora. (Gehörorgan von Amphicora, pp. 329–330.)
Zeitschr. wiss. Zool., III. (1851), 325–332.

IV. Marion, A. F.: Recherches Zoologiques et Anatomiques sur des Nematoides non Parasites, Marins. (Organes de l'Audition, p. 68–69.)
Ann. Sci. Nat. Zool., XII. (1870), Art. 14, pp. 100. Pl. XVI.–XXVI. (A–K of text).

V. Mecznikow, Elias: Beiträge zur Kenntniss der Chaetopoden. (Gehörorgan bei Fabricia, pp. 331–332.)
Zeit. wiss. Zool., XV. (1865), pp. 328–341. Taf. XXIV.–XXV.

VI. Quatrefages, A. de: Note sur l'Organe Auditif de la Marphyse Sanguine.
Ann. Sci. Nat. Zool., XI. (1870), 345–346.

VII. —— —— Études sur les Types Inferieurs de l'Embranchement des Annelés.
Memoire sur les Organes des Sens des Annélides. (Sens de l'Ouïe, p. 28.)
Ann. Sci. Nat. Zool., XIII. (1850), 25–41. Pl. II., figs. 16–19.

VIII. Siebold, C. Th. von: Ueber das Gehörorgan der Mollusken. (Zusatz ueber Gehörorgan der Arenicola, p. 166.)
Wiegmann's Arch., Bd. I. (1841), 148–168.

IX. Stannius, Hermann: Bemerkungen zur Anatomie und Physiologie der Arenicola piscatorum.
Müller, Arch., 1840, pp. 352–380. Taf. XI., fig. 1–15.
(S. 379 describes two *Knöpfen* containing crystals at the sides of the œsophageal ring-otocysts.)

Other papers might have been enumerated also, but there appeared to be little object in lengthening the list.

quently studied by Keferstein (II.) and Claparède.[1] In Nematods they have been observed to my knowledge only by Marion (IV.).

The entire series of observations is so fragmentary that we know nothing accurate concerning the minute structure of the organs under consideration, nor are we able to say how general their occurrence may be, nor yet whether, when they do occur, they are all closely similar or not. They present, however, an evident general likeness both with one another and with the otocysts of molluscs. Among *Vermes* they have as yet been found only in a few isolated Genera, for example, among Annelids only in a few genera of *Polychæta*. They may lie at the sides of the œsophagus (*Arenicola*, *Amphicorine*), or in the second segment more upon the dorsal side (*Amphiglena*, *Fabricia*); as regards the supposed otocysts of *Fabricia*, Metschnikow thinks they open exteriorly and doubts their being auditory vessels. Of the development of the otocysts nothing is known. When we consider that the ventral ganglionic cord of worms is, probably, homologous with the pedal ganglion of molluscs, it is at once evident that the relative positions of the otocysts are quite similar. Further, the minute anatomy is, as far as known, essentially the same in both subkingdoms. I think we must therefore conclude that the otocysts in these two great divisions are strictly homologous, and in a subsequent article it will, I think, be sufficiently demonstrated that this homology must be extended to include the vertebrates also.

Among the worms the otocystic walls are undoubtedly composed of a lining epithelium, which rests upon a fibrous *tunica propria*. They contain otoliths, usually several small ones (Nematods, Nemerteans, Arenicola, etc.), or rarely a single large one (Amphicorine). The otoliths tremble constantly. The nerve comes up to one side, but its origin is not satisfactorily determined; although it probably springs from the supra-œsophageal ganglion.

As Leydig's description of the otocysts of *Amphicora* is the best I have found of these vesicles in any worm, I quote it in full. It forcibly illustrates our imperfect knowledge, —

"Betrachtet man sich aber den unteren Gehirnknoten, so sieht man

[1] Beobachtungen ueber Anatomie und Entwickelungsgeschichte an der Küste Normandie angestellt.

ein Gehörorgan so schön und klar, wie bei Gasteropoden und auch von ganz gleichem Charakter. Schon ohne dass der Wurm mit einem Deckglas beschwert ist, wird es erkannt. Es zeigt sich als zwei Blasen, die 0.0135‴ gross sind und seitlich dem Gehirnknoten unmittelbar aufsitzen. In der Blase liegen gegen 20 Otolithen, welche dieselbe zitternde Bewegung ausführen, welche von den Gehörsteinen der Gasteropoden bekannt ist. Nur bezüglich der Otolithen lag darin ein kleiner Untershied vom Gehörorgan der Gasteropoden vor, dass sie nicht jene genane spindelförmige Gestalt hatten, sondern von mehr rundlicher oder auch unregelmässiger Form waren."

6. Median Otocyst of Turbellaria[1] and Tunicata.

As regards the otocysts of the *Turbellaria* it is to be expected that we shall ultimately be able to homologize them with the paired otocysts of molluscs and annelids. It is well known that in many crustacea the two eyes meet in the median line and fuse into a single organ. This fact suggests the possibility that in the *Turbellaria* the single otocyst may have arisen by the fusion of two vesicles; but this is merely a guess, since we know absolutely nothing of the development of the organ. The plausibility of this view is strengthened by the fact that one of the Rhabdocœla, *Sidonia elegans*, has two otocysts (Max Schultze).

The otocyst itself is a single round vesicle, placed directly over the brain. It has not been found in all forms, and on the other hand there are two smaller supplementary otocysts in a few species (Graaf). Concerning the histology of the vesicles nothing is really known.

[1] The term Turbellaria is here used in the restricted sense, *i. e.*, referring only to the Planarians (*Rhabdocœla* and *Dendrocœla*), or those members of the class of Plathelminths for which I have proposed the name of *Pharyngocœla* in an article on these animals, which was published in the third volume of Semper's Arbeiten. Of course, as the term is here used, the Nemertean worms are not included, and in fact it would be unscientific to do so.

The following are the principal authorities: —

Jensen, Olaf S.: Turbellarier ved Norges Vestkyst. (Pris-skrift.) Bergen, 1878, 4to. (Hœreorgan, p. 15.)

Schultze, Max Sigmund: Beiträge zur Naturgeschichte der Turbellarien. 4to. Greiswald, 1851. (Gehörorgan, pp. 25–26.)

Graff, Ludwig: Zur Kenntniss der Turbellarien. Zeit. wiss. Zool., XXIV., 123–160. Taf. XIV.–XIX. (Gehörorgan, p. 138.)

The otoliths have been somewhat more studied. There is usually a single round stone, but in some species of *Monocelis* there are two small outgrowths from the main stone, while in *Aphanostomum* there are four such. These additional parts are described as separate stones united with the main large one. If a round otolith is crushed it shows a tendency to cleave into a central part and outer zone (Jensen). The central portion exhibits a cross-shaped figure sometimes very distinctly.

Passing to the otocysts of *Tunicates*, we find the data as unsatisfactory as in the case of the low worms we have just reviewed. Our knowledge is based principally upon the observations of Kowalewski, Kupffer, Fol, and Ussow.[1] The researches of the last mentioned author appear to be particularly important, so that it is a matter of regret that they are published in Russian, which language I am unable to read.

In the tailed Ascidians (Appendiculariæ) there is a single otocyst of which Fol gives the following description: "Sur le coté gauche du Ganglion est située la vesicule auditive, presque sphérique, et renfermant une concrétion également sphérique. J'ai aperçu quelquefois de fines soies isolées les unes des autres et qui suspendaient l'otolithe à la paroi de la vésicule." Kupffer has described the epithelial cells and stiff hairs of the wall. In other forms there are two otocysts symmetrically placed (*Doliolum*, etc.), but concerning the development and homologies of these paired organs, I have found nothing — although Ussow may have something about it. In the

[1] Kowalewski: Entwickelungsgeschichte der einfachen Ascidien. Mém. Acad. St. Petersb., X. No. 15 (1866), pp. 19. Taf. I.–III.

——— Weitere Studien über die Entwickelung der einfachen Ascidien. Arch. f. m. Anat., VII. (1871.)

Kupffer, E.: Die Stammverwandschaft zwischen Ascidien und Wirkelthieren. Arch. f. mikros. Anat., VI. (1870.)

——— ———. Zur Entwickelung, der einfachen Ascidien. Arch. f. mikros. Anat., VIII. (1872.)

Fol, H.: Études sur les Appendiculaires du Détroit de Messine. Mem. Soc. Phys. d'Hist. Nat. Genève, 1872.

Ussow, M. M.: Beiträge zur Kenntniss der Organisation dor Tunicaten. Nachrichten Moskau Univ., XVIII. Hft. 2, (1876), pp. 62, 9 Taf. (In Russian, quoted here from Hoyer.)

simple Ascidians, the auditory organ is developed from the lower floor of the cerebral vesicle. As Balfour, in his "Comparative Embryology," vol. ii., p. 437, gives a very clear description of the development and structure of the organ, I quote his account, which is based upon the researches of Kowalewski and Kupffer. Balfour commits the error of making his statements apply to all the tunicates, whereas in fact they apply only to the simple Ascidians. The auditory organ "consists of two parts, (1) a prominence of the cells of the floor of the brain, forming a crista acustica, and (2) an otolith projecting into the cavity of the brain, and attached to the crista by delicate hairs. The crista acustica is formed of very delicate cylindrical cells, and in its most projecting part is placed a vesicle with clear contents. The otolith is an oval body with its dorsal half pigmented and its ventral half clear and highly refractive. It is balanced on the highest point of the crista. The crista acustica would seem to be developed from the lower part of the front vesicle of the brain. The otolith, however, is developed from a single cell on the dorsal and right side of the brain. This cell commences to project into the cavity of the brain, and its free end becomes pigmented. It gradually grows inwards till it forms a spherical prominence in the cavity of the brain, to the wall of which it is attached by a stalk. At the same time it travels round the right side of the vesicle of the brain (in a way not fully explained) till it reaches the summit of the crista, which has become in the mean time established." The development presents a close and striking analogy in the simple Ascidians with that of the ear. The crista and otolith are derived from the cerebral vesicle. In no other animals are the auditory organs known to have a similar origin.

7. Auditory Hairs of Crustacea.

The *Crustacea* have, as far as at present known, no organs homologous with the otocysts of other invertebrates. But their skin bears peculiar hairs, that are evidently sensory in function, since they are connected with nerve filaments. One form of these hairs, found hitherto only in the higher forms of the class, have been assigned the office of audition, although absolute proof thereof is, I think, still to

be given. In order to give a clear account of these structures, we prelude a brief description of the skin and hairs in general, the hairs having *no* resemblance to those of vertebrates.

The epidermis, or true ectodermal skin, of arthropods, is a single layer of cells — a cylindrical epithelium. Upon this rests the thick crust or cuticula, which, as is well known, is composed mainly of chitine, and is secreted by the action of the underlying epithelium. From place to place the cuticula is pierced by very small vertical openings; the so-called pore-canals. These do not, however, open upon the exterior, but are covered over by a projecting hollow process of the cuticula, making a minute tapering hair (Fig. 14). The cavity of the chitinous hair-tube is filled by a protoplasmatic process, which comes up through the pore-canal, and arises upon a cell-body lying right under the pore-canal. The hair cells are of larger size than the unmodified cells of the epidermis, and contain usually several large and conspicuous nuclei. It is possible that each hair-cell is in reality a cluster of cells, as some authors have maintained; but it is more probable that we have to do exclusively with unicellular structures. The hairs are tapering, of various sizes and forms. They are generally, if not always, constricted around the base, and are connected by a thin cuticular membrane with the outer edges of the pore-canal. Hence we have a stiff hair movable from its base acting as an articulation. The hairs are in many instances provided with secondary lateral branches, thus imparting to these simple structures a likeness to feathers.

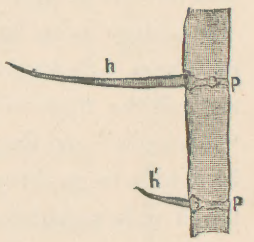

FIG. 14. Grasshopper, *Caloptenus*. Section of cuticula. *p*, pore-canal; *h*, *h'*, hairs.

The chitinous hairs play an important part in the physiology of Arthropods. We find them assuming olfactory functions in the antennæ, and undergoing corresponding structural modifications. Indeed, such olfactory cells have several times been mistaken for auditory organs by entomologists, an error which has only recently been set aside. Compare the closing paragraph of this article.

In the Crustacea, certain of the hairs are thought to perform the function of audition; but this, as before stated, requires further and

more rigorous demonstration. The supposed auditory hairs present marked structural peculiarities, and occur either isolated or clustered at special points, namely, the base of the inner antenna in the higher Decapods, and in the inner swimmeret of the tail in Schizopods (*Mysis*). The clusters are invaginated so as to form either open pits or closed vesicles, which may be fairly termed otocysts, and may contain special bodies — otoliths.

We shall, therefore, pursue the following order of treatment: First, the general character of the auditory hairs; second, their distribution; third, the peculiarities of the invaginated clusters, including the shape of the invaginations; and fourth, the otoliths; finally, a few words will have to be added concerning the nerves.

Auditory hairs have hitherto been described only in the higher crustacea (*Podopthalmata*) and *Hyperida*, a family of Isopods. As regards the *Hyperida*, I repeat merely the statement found in Claus' "Zoologie" and Gegenbaur's "Comparative Anatomy." I have not been able to go through the original papers properly. As yet I have found only a doubtful description by Kröyer, which Hensen was unable to confirm. Claus, in his "Grundzüge" (3d edition, p. 517), in giving the characters of the Hyperina, "Ein paariges Gehörbläschen ueber dem Gehirn (*Oxycephalus*, *Rhabdosoma*)." It is possible that similar hairs will be found in the lower forms also, whenever investigation shall turn to the solution of that question. There are many Phyllopods which bear upon their antennæ a number of hairs, exhibiting marked specializations and in some cases known to receive a nerve filament. In these animals the functions of such hairs have been currently assumed to be either olfactory or tactile, although such interpretations rest upon a basis purely subjective. When actual observation shall have decided what purpose is subserved by these often described appendages it will perhaps be found that they are auditory in function.

On the other hand, certain hairs of Isopods have without sufficient foundation been considered auditory in function. Leydig[1] described in 1860 some peculiar transparent feathered hairs on the inner an-

[1] Leydig, Franz: Ueber Geruchs- und Gehör-organe der Krebse und Insekten. Arch. f. Anat. Physiol. 1860.

tennæ of *Asellus aquaticus;* to these hairs Sars [1] and Ritzema Bos assigned afterwards auditory functions. Similar hairs occur on other Isopods. Recently Leydig [2] expresses himself unfavorably to Sars' interpretation. Rabl-Rückhard in a brief article [3] sides with Leydig, on the ground that the hairs swing readily to and fro with the wave motions of the water, and show no tendency, as far as he observed, to make real sound vibrations. He suggests that they may serve to perceive the disturbance produced in the water by an approaching animal. This view possesses considerable plausibility; and certainly we lack positive information concerning the auditory organs of Isopods. The hairs in question (Fig. 15) occur on the antennæ, legs, and tail. They are rather long with a straight, smooth, tapering shaft, slightly enlarged at its base, and bearing at its top a bunch of very fine hairlets spread out fanlike.

FIG. 15. *Asellus aquaticus* "*Büschelhaar*," or supposed auditory hair of antenna.

Our knowledge of the auditory hairs is due to Farre, Leuckart, and others, but especially to Hensen, whose results, however, sorely demand amplification and to some extent verification. Unfortunately his article is a slovenly composition, and though his observations are valuable he has presented them in so disorderly a manner that it has cost an exasperating amount of labor to get his data into a presentable form.

The auditory hairs of Crustacea are modifications of the indifferent hairs described above. They present the following features in common with one another (Fig. 16).[4] Above the basal constriction the cuticula of the hair is quite thin and forms a bulb of greater diameter than the remaining shaft, which is also distinguished by having a thicker chitinous envelope. The outer edge of the pore-canal forms a thickened ring from which springs on one

[1] SARS, G. O.: Histoire naturelle des Crustacés d'Eau douce de Norvège. (Soies auditifs, Gammarus, p. 62, Asellus, pp. 95 and 112.) Christiani, 4to, 1868.

[2] LEYDIG: Zeit. f. wiss. Zool., XXX. (Suppl.), 251.

[3] RABL-RÜCKHARD: Ueber die Hörhaare der Isopoden, besonders des Asellus aquaticus. Sitz. ber. Nat. forsch. Freunde, Berlin, 1878, 148–151.

[4] Our knowledge is so fragmentary that a general description can only be approximative, and may hereafter need rectification.

side a projecting thickening that enters into the composition of the bulb. Hensen has named this part the "tooth." It might also be described as a local thickening of the one side of the basal enlargement. Opposite to the tooth there is a longitudinal, rib-like thickening of the cuticula of the shaft, called the *lingula*. The lower end of the *lingula* projects into the cavity of the bulb.

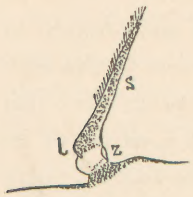

FIG. 16. Crangon vulgaris. Auditory hair. *z*. Henson's Tooth; *l*. lingula.

Concerning the cells (Trichogens) which belong to the auditory hairs, we possess no knowledge. Hensen's description of the hair-making cells obviously refers not to the Trichogens, or true hair cells, but to modified parts of the epidermis.

As regards the distribution of the hairs: The free hairs occur principally in two regions at opposite ends of the body. They have been most fully studied in the *Caridea* (shrimps and prawns) and in *Mysis*. We refer, therefore, principally to these forms. They are placed *first*, on the basal joints of the inner antennæ and also a few on the outer antennæ; *second*, on the tail or last segment. Their number and distribution varies according to the genus and somewhat also according to the species. In an adult *Palæmon antennarius* there are about five hundred, of which about two hundred and fifty belong to the antennæ, the remainder to the lateral tail swimmerets. The number appears to increase somewhat with the age of the individual. There is a marked tendency for the hairs to collect in little groups, or more especially curving rows.

The clusters of hairs found in the invaginations may be regarded as a group of hairs, such as we have just signalized, but distinguished by accompanying accessory modifications. Auditory pits occur at both ends of the body. In the *Decapods* the pit or sack lies in the basal joint of the inner antenna, but in the *Schizopods* is placed in the inner lappet or swimmeret of the caudal fin. In *Thysanopoda* sp? there are three transverse rows of "Hörhaare" on the basal joint of the inner antenna, representing, perhaps, the condition in which the cluster on the joint has been formed but not invaginated.

In the regions of the inturned clusters (otocysts) the cuticula of

the skin, which of course forms the limiting wall of the cavity, is much thinner than on the exposed parts of the body. The pore-canals at the base of the hairs are usually quite wide, and their course through the cuticula is nearly vertical to the surface, although sometimes oblique as is found to be the case in *Palæmon*. The basal bulb of the hairs is less distinct than in the free hairs of the surface, and in the highest forms, crabs, can be recognized only obscurely. It is said that the *Lingula* and Hensen's "*Zahn*" can always be detected, but Hensen's figures represent those points imperfectly. The shaft is always tapering, and varies greatly in length, reaching its maximum extension in the crabs (see below). In the simpler forms the hairs are nearly straight or at most only slightly curved; such hairs occur in *Astacus* and *Crangon*. The first specialization met with is the bending of the hairs at a marked angle. This modification is found in *Palæmon*, but, curiously, not in the closely allied genus *Crangon;* again in *Mysis* and *Leucifer*, in both which the bent ends penetrate the body of the otolith.

In the *Brachyura* and several *Macroura* (*Porcellana*, *Gelasimus*, etc.), there is a clear advance of organization in that three distinct kinds of hairs are developed in the antennal vesicle: in the crab there are first, simple curved hairs, lying in one cluster; second, another cluster of short bent hairs; and third, a single row of long hairs with just the tip bent and a short spine-like continuation of the shaft beyond the angle of the bend. Curiously enough only hairs similar to this last kind were observed by Hensen in the crab larva (Zoëa).

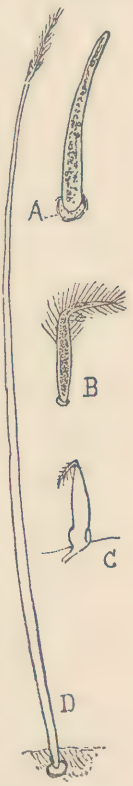

FIG. 17. Crustacea: various forms of auditory hairs. *A*, *B*, *D*, Carcinus mænas; *C*, Mysis.

The feathering of the hairs likewise varies considerably, but we cannot say at present which variety is the primitive nor which are the derived forms. It will be convenient to call the secondary tapering shafts, that arise from the main stem and produce the feathering, *hairlets*. The hairlets are wanting in *Mysis*, but are found on the majority of hairs in the vesicles. They rarely attain a length greater than one fifth of that of the main shaft. They are confined to the

distal end of the shaft and may extend more or less than half way down its length. They may arise either irregularly, or spring from a spiral line (*Astacus*) or become more like the barbs of feathers by growing out along two longitudinal lines on opposite sides of the hairs, or, again, in a double longitudinal row on one side only (*Crangon*).

We take up next the form of the auditory vesicles and the disposition of the hairs in them. We begin with the antennal organs of Decapods and will consider the caudal apparatus of *Mysis* separately. To both structures is common the characteristically thin cuticula.

The antennal otocyst of Decapods is situated on the upper side of the basal joint of the inner antenna. The basal joint is itself often enlarged; in the crabs greatly so (Fig. 18). The relative size of the invagination also varies extensively. In its simplest form the otocyst is a widely open pit (*Palinurus*), the opening being closed by hairs, as may be well seen in *Crangon*. In other forms the opening is reduced to a narrow fissure, which may then be partially closed as in *Palæmon* by an overlying valve-like flap of the integument. When the entrance to the pit is narrowed the opening usually comes to lie towards the inner side and distal end of the joint. A step further and the pit becomes entirely closed over (*e. g.*, *Hippolyte*). In all the Decapods except the crabs (*Brachyura*) the otocyst varies but slightly from the simple rounded form. In the crab larva they still preserve their simple shape; concerning their configuration during the second larval stage, the megalops, I have found no statements; in the adult important modifications supervene in the shut vesicle by the formation of projections and recesses on the medial walls, and of thickened knots and ridges of the cuticula of the lateral walls; these last serve for the attachment of muscles. For the minutiæ we must refer the reader to Hensen's somewhat lengthy and confused description. An approach towards the complexity of form in the crabs is found in the prawn *Alpheus*, in which the otocyst is divided into an anterior smaller part, and a posterior larger part containing the otolith. The

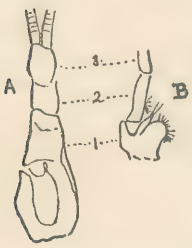

FIG. 18. Inner antennæ. *A.*, of lobster; *B.*, of *Palinurus*.

hairs in the two divisions are different, those in the posterior being bent.

As regards the disposition of the hairs in the otocysts there appears to be a general tendency to form curving rows, which may extend to make a complete circle. The rows may be single or double. There may be several concentric rows; sometimes there is a central cluster of hairs. This is, however, by no means the only system of arrangement; thus in *Sergestes Atlanticus* there are two longitudinal rows, and, crossing them, three tranverse rows. But it must be added that there exists at present no adequate basis for a general comparative description. Unfortunately Hensen's article is almost innocent of generalizations, being entirely devoted to detail, a striking instance of what Mill has called reasoning from the particular to the particular, — so that the mental labor to utilize his investigations has to be supplied entirely by the reader. In the crabs, as above mentioned, there are three kinds of hairs: the simple curved hairs lie in the outer corner of the sac; the short bent hairs occupy the posterior corner (Hensen's *Otolithen-platz*), which is further characterized by being pierced by large and conspicuous pores, which are supposed to serve as ducts for underlying unicellular glands; the long bent hairs arise along a line extending from below laterally upwards. (Cf. Fig. 18.)

The otocyst of *Mysis* and other Schizopods is an invagination of the upper surface of the inner swimmeret of the tail. It is an oval vesicle (Fig. 19), compressed in its vertical diameter and most flattened on the under side, which receives the nerve, supports the oblate otolith, and bears the circlet of auditory hairs, that encompass the otolith. (Fig. 19.) The opening is a narrow oblique slit, partly covered over by a flap-like growth of the integument, and lies near the outer or lateral edge of the upper surface of the lamella. The organs under consideration are so conspicuous that there are many incidental references to them in the descriptions of species, so that I much regret not to have had at my disposal the time necessary to cull

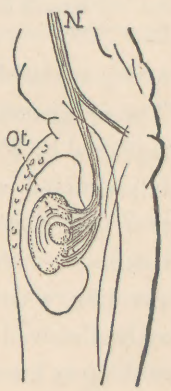

Fig 19. *Mysis*. Otocyst in inner swimmeret of tail. *n*, nerve; *ot*, otolith.

these data from the writings in which they are scattered. The hairs form about two thirds of a circle around the base of the large otolith, making an open bow ; near the ends of the bow the hairs are disposed in a single row; but towards its centre in double or treble lines. As before stated, the ends of the hairs are all bent, curving over towards a common centre, the bent tips penetrating little holes in the substance of the otolith, which is otherwise unsupported.

Otoliths are found in the auditory pits or sacks in all species, with the exception of the crabs. They are of two kinds: *first*, foreign bodies, such as grains of sand or small crystals introduced from outside, — such are found in the long-tailed Decapods (*Macroura*) with open otocysts ; *second*, a single large (organic?) growth, found in the antennal sacks when closed and in the caudal sacks of Schizopods.

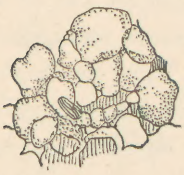

Fig. 20. Sand grains from the antennal ear of the craw-fish.

In the first case the otoliths are a mass of foreign particles, usually grains of sand (Fig. 20), which are introduced anew after each moult; hence, if the animal, a prawn or crawfish for instance, passes through its moult in clean water with no foreign particles there are no otoliths in the vesicle after the moult; again, if instead of sand grains, crystals of uric acid are put in the water, the crystals are found acting as otoliths. The animal probably always introduces them itself. The indigenous otoliths, on the other hand, are each a single mass, supposed by Frey and Leuckart to consist at least in *Mysis* of chitine impregnated with lime salts. Hensen, on the contrary, maintains that they contain no chitine but are built up almost entirely of chalk combined with some acid. Neither view applies to the otolith of *Leucifer*, which cannot be either chitine or chalk, since it is immediately dissolved by caustic alkali and hydrochloric acid. Absolutely nothing is known of the development of the otolith. In the closed otocysts it may be supposed to remain permanently, when once formed. In the Schizopods, on the contrary, it is cast off with every moult, and rapidly reformed in a manner as yet undetermined. As regards the size of the otolith, it may be roughly indicated by fixing its diameter as usually more than half that of the sack. It is always rounded in shape. The only minute description of the structure we

possess refers to *Mysis*. In this genus the otolith is a thick rounded disk, the lower surface flattened, the upper convex with a slight prominence. It has a granular centre ; a strongly marked line, dividing off an outer layer from an inner layer around the granular core ; the outer layer is pierced by fine holes occupied by the bent ends of the auditory hairs ; it shows radial lines, and also concentric lines indicating a laminar structure ; these last mentioned markings are not very distinct nor always parallel with the surface, but bend out and in as if yielding to the entering hairs.

It remains only to describe the connection of the hairs with the nervous system. Here we must rely exclusively upon Hensen, whose account refers to several structures, the morphological nature of which he has probably misinterpreted ; the structures in question are a fine thread, named *chorda* by Hensen, which arises from the *lingula* of the hair, passes down through the pore-canal some distance in a straight course into the underlying tissues ; and second, a sheath enclosing the thread. The lower end of the thread is said to become continuous with a ganglion cell, which in its turn is the termination of a peripheral nerve fibre. That the thread itself is a nerve filament is rendered doubtful by Hensen's assertion that it is sometimes pulled out with the hair, and remains straight and stiff, having none of the frailness and flexibility of nervous tissue ; moreover it resists the action of caustic alkali. As to what the sheath may be Hensen's observations afford not the slightest clue. Further investigations are urgently needed.

The process of moulting the hairs presents various peculiarities, which Hensen describes, but, unfortunately, with so total a disregard of the structure of the skin that his account can only be partially comprehended. We will therefore only mention that the cuticula of the hair is shed, a new cuticula being formed in the basal part of the old hair and partly inside the crust, as shown in the diagram. The traces of the old thread (*chorda*) may be seen in the old hair, while the new one is also visible.

In the so-called tympanal organs of the insects, the nerve fibre ends with a ganglion cell, from which runs out a peripheral process containing a hard rod, "*Stäbchen*." These organs, which will be de-

scribed in the next article, present, therefore, an evident resemblance to the nerve endings of the hairs as given by Hensen. Whether there is any real homology between them the future must decide.[1]

Several authors [2] have described the sensory hairs on the antennæ of insects as auditory, but apparently without justification — and recently the olfactory function of these hairs has been quite satisfactorily demonstrated.[3] Curiously enough they sometimes form invaginated groups, producing a vesicle with hairs projecting into it, and thereby acquiring a deceptive resemblance to otocysts. Indeed, Graber was misled by these pits in the common flies (*Muscidæ*) into terming them *otocystenartige Organe.*

[1] Hensen, V.: Studien ueber das Gehörorgan der Decapoden. Zeitschr. f. wiss. Zool., XIII. (1863), 319–412. Taf. XIX.–XXII.

[2] Graber, Vitus: Ueber neue otocystenartige Organe der Insekten. Arch. f. mikros. Anat., XVI., 1878, p. 36. (Gives also the previous literature.)

Mayer, P.: Sopra certi organi di senso nelle antennæ dei Ditteri. Mem. Accad. Lincei Roma. 4 Maggio, 1879.

[3] Hauser, Gustav: Physiologische und histiologische Untersuchungen ueber das Geruchsorgan der Insekten. Zeit. f. wiss. Zool., XXXIV., 367–403. Taf. XVII.–XIX. (1880).